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Warming experiments underpredict plant phenological responses to climate change

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Warming experiments are increasingly relied on to estimate plant responses to global climate change[1, 2]. For experiments to provide meaningful predictions of future responses, they should reflect the empirical record of responses to temperature variability and recent warming, including advances in the timing of flowering and leafing[3, 4, 5]. We compared phenology (the timing of recurring life history events) in observational studies and warming experiments spanning four continents and 1,634 plant species using a common measure of temperature sensitivity (change in days per degree Celsius). We show that warming experiments underpredict advances in the timing of flowering and leafing by 8.5-fold and 4.0-fold, respectively, compared with long-term observations. For species that were common to both study types, the experimental results did not match the observational data in sign or magnitude. The observational data also showed that species that flower earliest in the spring have the highest temperature sensitivities, but this trend was not reflected in the experimental data. These significant mismatches seem to be unrelated to the study length or to the degree of manipulated warming in experiments. The discrepancy between experiments and observations, however, could arise from complex interactions among multiple drivers in the observational data, or it could arise from remediable artefacts in the experiments that result in lower irradiance and drier soils, thus dampening the phenological responses to manipulated warming. Our results introduce uncertainty into ecosystem models that are informed solely by experiments and suggest that responses to climate change that are predicted using such models should be re-evaluated.

Subject terms: Ecology • Climate science

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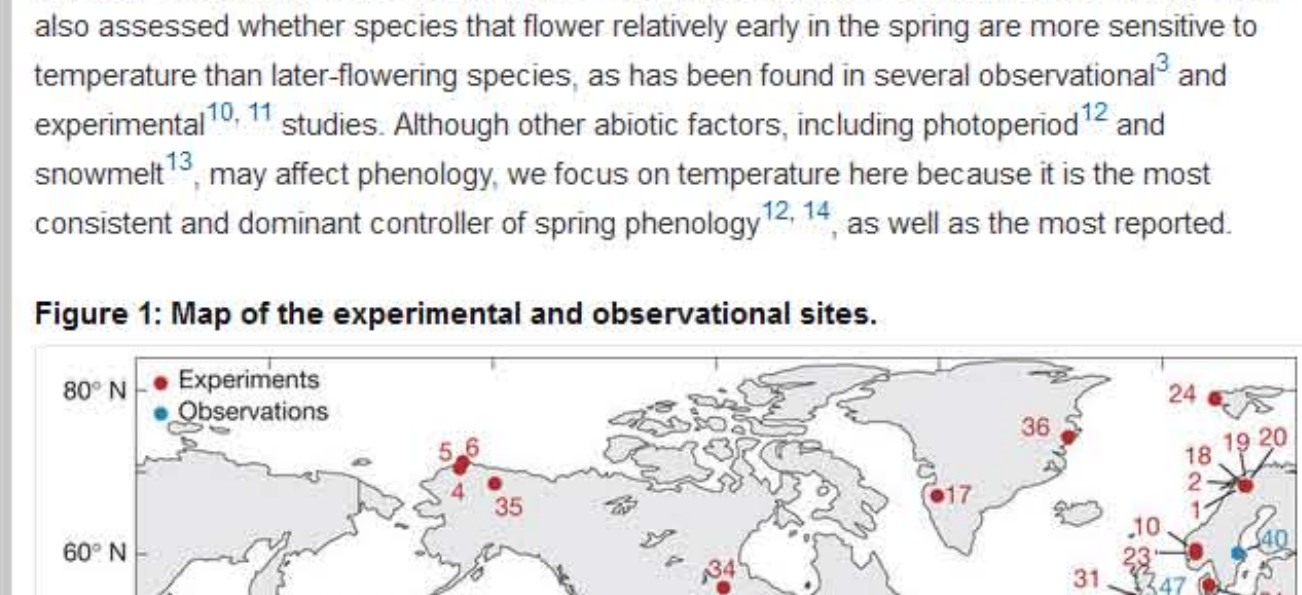
Predicting species' responses to climate change is a major challenge in ecology. Plants have been a focus of study because their responses can affect entire food webs, disturbance regimes and crucial ecosystem services, including pollination, carbon and nutrient cycling, and water supply[6]. Researchers have adopted two main approaches to predict plant responses to climate change. The first approach relies on observations over time or space to quantify sensitivities to temperature variability and climate change, including recent warming that is at least partly associated with greenhouse gas emissions[3, 4, 5]. The second approach relies on experiments that directly warm natural plant communities on a small scale[2, 7]. Results from both methods suggest that advancing phenology (for example, earlier flowering and leafing) is one of the most sensitive plant responses to warming. Current estimates of changes in phenology are 1.9–3.3 days per °C for experiments[1] and 2.5–5 days per °C for observations[3, 8].

Warming experiments have been used to extrapolate to future climate conditions for more than 20 years[7, 9]. This approach rests on the critical but little-tested assumption that plant responses to experimental warming match long-term responses to global warming. Testing this assumption is an important first step in assessing the utility of warming experiments for long-term forecasting and prediction. Recent studies have compared experimental and observational results at single sites[2, 10], and one study found coherence across methods in plant responses to warming[10], however, cross-site comparisons have proved more challenging.

Here we present two new spatially and temporally extensive databases of plant phenology for 1,634 species based on long-term observations and short-term warming experiments (Fig. 1). The databases were developed specifically to test how accurately short-term warming experiments predict the long-term responses of wild plants. We tested for differences in the overall estimated phenological sensitivity to temperature (change in flowering or leafing date per °C, hereafter referred to as 'temperature sensitivity') between the experiments and the observations. The sensitivities for each species at a site, *i*, were calculated as the β coefficient from the following: phenological event date$_i$ = β_i(MAT) + ε_i, where MAT is the mean annual temperature for each site and ε is error. Our observational sensitivities are thus based on interannual temperature variability. For the sensitivities from experiments, we used a regression approach similar to the observational calculation, which simplifies to the following: (phenological event date$_{i,\mathrm{warm}}$ − phenological event date$_{i,\mathrm{control}}$)/Δ*T*, where Δ*T* is the change in the temperature reported between the warmed and the control plots (Supplementary Information). We looked at how the sensitivities to temperature varied across space and time, and we tested whether sensitivity increases with latitude[5] or with the magnitude of temperature change[8]. We also assessed whether species that flower relatively early in the spring are more sensitive to temperature than later-flowering species, as has been found in several observational[3] and experimental[10, 11] studies. Although other abiotic factors, including photoperiod[12] and snowmelt[13], may affect phenology, we focus on temperature here because it is the most consistent and dominant controller of spring phenology[12, 14], as well as the most reported.

Figure 1: Map of the experimental and observational sites.



The map covers 14 long-term observational phenology studies and 36 experimental phenology studies (one experimental study site, in Australia, is not shown). The numbers correspond to site information given in the Supplementary Information.

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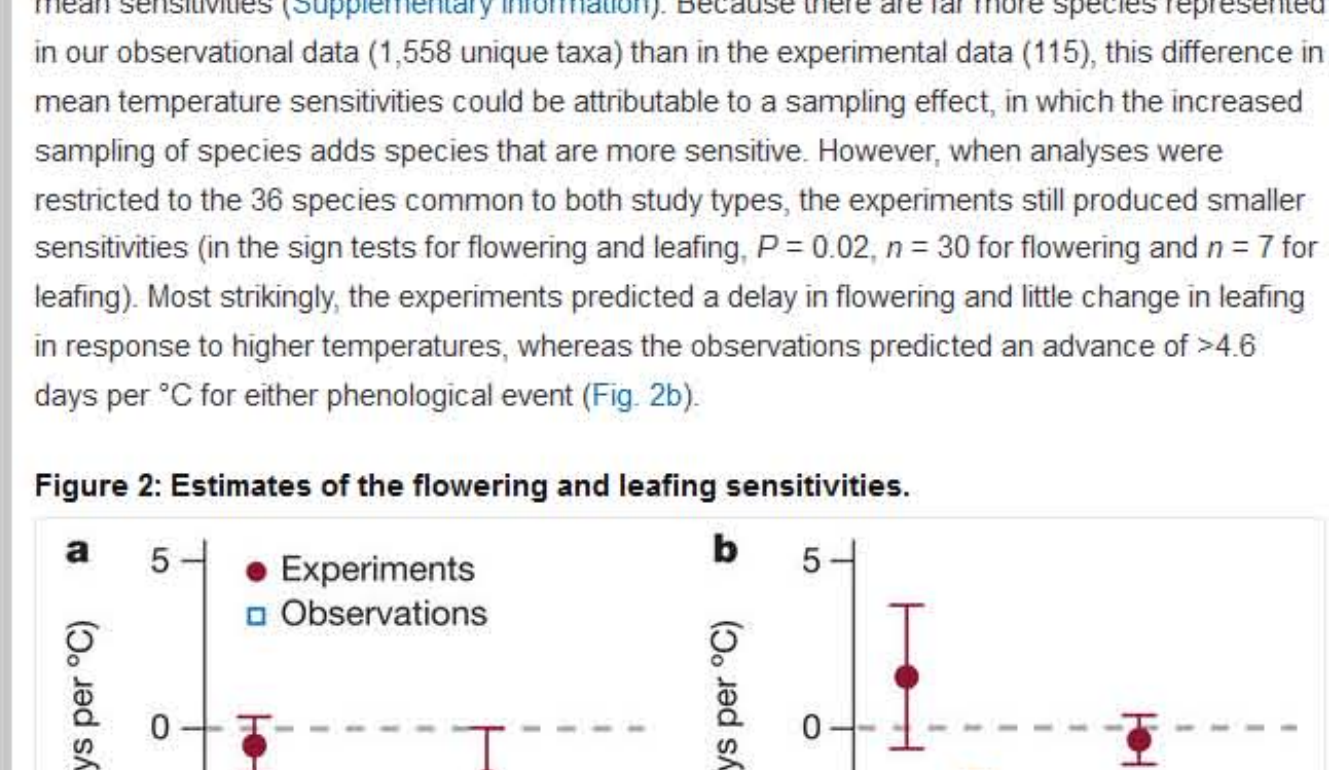
Warming experiments underpredicted observational responses to climate change (Fig. 2). Across all species, the experiments underpredicted the magnitude of the advance—for both leafing and flowering—that results from temperature increases (Fig. 2a; flowering, $F_{1,34}$ = 9.7, *P* = 0.004; leafing, $F_{1,18}$ = 2.8, *P* = 0.1). The estimates for observations were based on plant responses to interannual temperature variability, yet they were similar to estimates calculated from long-term trends (Fig. 3) and were consistent across alternative approaches to calculating mean sensitivities (Supplementary Information). Because there are far more species represented in our observational data (1,558 unique taxa) than in the experimental data (115), this difference in mean temperature sensitivities could be attributable to a sampling effect, in which the increased sampling of species adds species that are more sensitive. However, when analyses were restricted to the 36 species common to both study types, the experiments still produced smaller sensitivities (in the sign tests for flowering and leafing, *P* = 0.02, *n* = 30 for flowering and *n* = 7 for leafing). Most strikingly, the experiments predicted a delay in flowering and little change in leafing in response to higher temperatures, whereas the observations predicted an advance of >4.6 days per °C for either phenological event (Fig. 2b).

Figure 2: Estimates of the flowering and leafing sensitivities.



The estimates from the mixed effects model (presented as mean±s.e.m.), including the random effects of site and species, show that experiments underpredict the magnitude of plant responses to interannual temperature variation for all species sampled (**a**) and for the species that are common to both the experimental and the observational data sets (**b**). The region above the dashed grey line represents positive sensitivities, meaning that the species' phenological events are delayed with warming, whereas the region below the line represents negative sensitivities, meaning that the species' events advance with warming.

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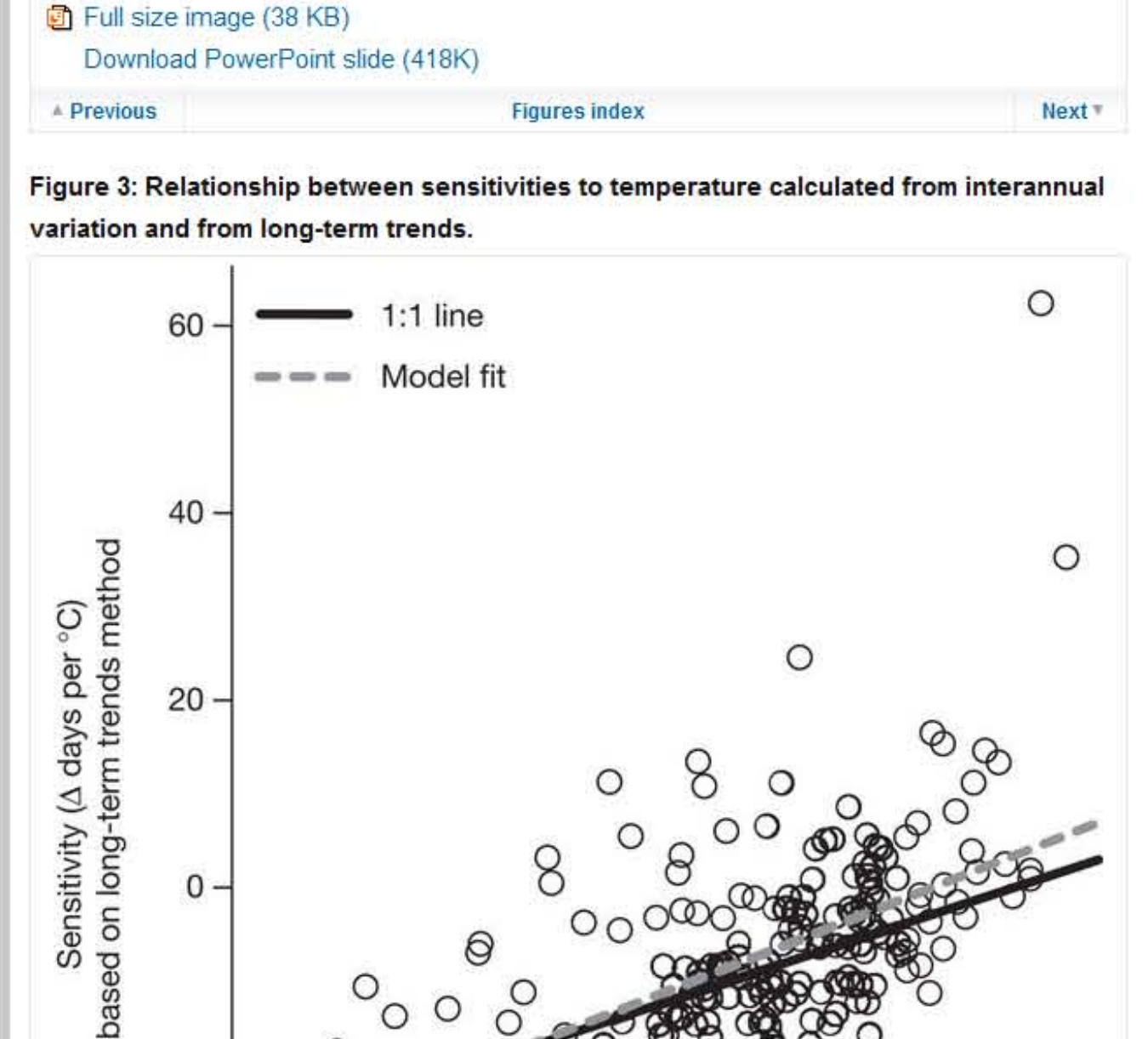
Figure 3: Relationship between sensitivities to temperature calculated from interannual variation and from long-term trends.



Observational sensitivities calculated from interannual variation (regression of flowering date versus MAT) were strongly correlated with those calculated from long-term trends (long-term trend in the flowering date versus long-term trend in MAT). The mixed effects model fit ($F_{1,185}$ = 63.9, *P*<0.0001) and the 1:1 line are both shown. For long-term sensitivity estimates, we used the subset of the NECTAR data corresponding to species with observations between 1971 and 2000 (a common standard for long-term climate trend analysis). See the Supplementary Information (Observational sensitivities: comparisons with long-term trends and 1971–2000 standard) for complete details and for further alternative methods and data for calculating observational sensitivities.

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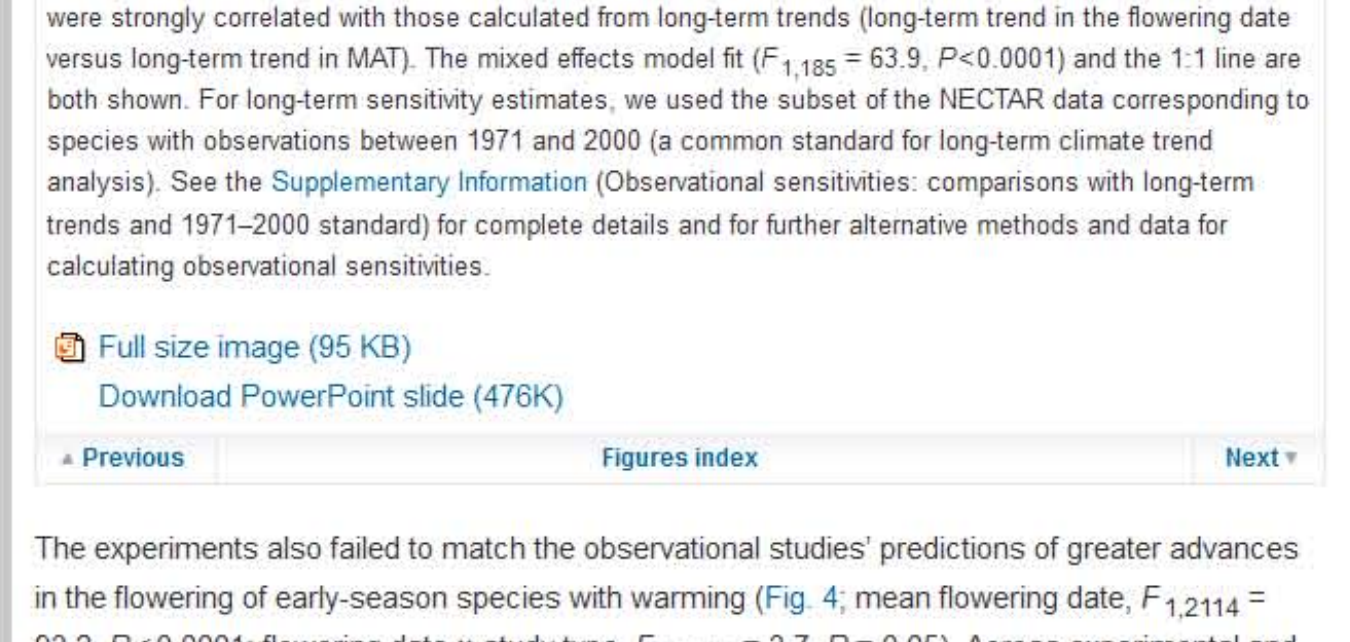
The experiments also failed to match the observational studies' predictions of greater advances in the flowering of early-season species with warming (Fig. 4; mean flowering date, $F_{1,2114}$ = 93.2, *P*<0.0001; flowering date × study type, $F_{1,2114}$ = 3.7, *P* = 0.05). Across experimental and observational study types, sensitivities were not associated with latitude ($F_{1,31}$ = 0.02, *P*>0.8) or interannual climate variability ($F_{1,31}$ = 0.1, *P*>0.7), suggesting that, although the interspecific variation in sensitivities is great, communities that are governed by different climate regimes do not differ in their overall sensitivity to warming. Additionally, we found no evidence that sensitivities varied with the degree of experimental warming ($F_{1,76}$ = 1.1, *P* = 0.3); this is in contrast to the observational studies, which show an increase in sensitivities with the degree of warming (Supplementary Information; $F_{1,4856}$ = 12.3, *P* = 0.0005; see also ref. 8).

Figure 4: Sensitivity to temperature decreases throughout the growing season.



This trend is seen in the observational studies (blue) but not in the experimental studies (red). The numbers correspond to those in Fig. 1 and to site information given in the Supplementary Information. The linear model fitted to the observational data predicts that species blooming 3 months apart would have differences in sensitivities of >3 days per °C. Exp, experimental data; Obs, observational data.

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Several artefacts might explain the lower sensitivities in the experimental studies, including differences in the traits of the species sampled, correlations between MAT and other environmental variables for the observational studies, and differences in the degree of warming. We found no evidence, however, that these factors explain the smaller or positive sensitivities found in the experiments. Both study types mainly examined longer-lived plant species (85.0% and 88.4% were perennials in the experiments and the observations, respectively), and most were herbs or forbs (78.0% and 72.3%, respectively) not woody species (Supplementary Information). In addition, we found no correlations between MAT and other climate variables for which data were available (Supplementary Information). Finally, both study types spanned roughly a 0–5 °C temperature range, with a median of 1.4–2.4 °C (Supplementary Information).

Given the difference in time frames between the experimental and observational studies (3.8 years and 31.0 years, respectively; $F_{1,49}$ = 72.0, *P*<0.0001), the experiments may capture predominantly plastic responses to temperature change, whereas the observational studies may also integrate shifts in genotypes, community composition and ecosystem dynamics. Furthermore, plant responses may have shifted fundamentally following the significant Northern Hemisphere warming in all seasons starting in the 1970s[15], thus the experiments (which have been conducted relatively recently) may capture only these shifted dynamics. However, we found that these scaling issues would create a bias towards detecting greater sensitivities from short-term, post-1970 studies (Supplementary Information), which is opposite to the trends in the experimental studies. Sensitivities that captured 31–35 years of phenological change were generally smaller than those that spanned 5 or fewer years (sign tests of *P*≤0.02, Supplementary Information). In addition, the sensitivities were similar before 1970 and after 1970 (*P*>0.1, Supplementary Information), when warming trends began to accelerate[15].

Although warming methods have continually improved[16, 17, 18], all experimental manipulations unavoidably alter additional environmental factors. For example, the most common passive warming structures—open-top chambers—reduce light, wind and often soil moisture and can unintentionally increase minimum winter temperatures[19, 20]. By contrast, above-canopy heaters, which are common structures for active warming, often achieve warming only in periods of low wind[17]. We found no evidence of differences in the sensitivities between the passive and active designs ($F_{1,23}$ = 0.05, *P*>0.8). Designs using above-canopy heating, however, tended to produce the greatest phenological advances for flowering (Supplementary Information; $F_{2,22}$ = 7.2, *P* = 0.004), and this was the type of heating used in the one study that found correspondence between experimental and observational methods[10] (Supplementary Information). There were no effects of habitat (for example, alpine or arctic), study duration or period of warming each year (Supplementary Information): the results from studies that manipulated temperature only during the growing season were indistinguishable from those that elevated temperature year round ($F_{1,18}$ = 0.5, *P*>0.4). Both active and passive experimental designs tend to reduce total irradiance and soil moisture[11, 19, 21], which can delay plant phenology[2, 22]. Thus, the lower sensitivities of the experiments could be the product of planned temperature increases that tend to advance phenology and artefacts that tend to delay phenology. Alternatively, the lower sensitivities of the experiments could occur if experimental studies isolate temperature effects, whereas observational data integrate the effects of complex and possibly reinforcing interactions among multiple drivers of anthropogenic climate change and variability (Supplementary Information).

One needed improvement for both experimental and observational studies is the increased reporting of temperature and other relevant environmental metrics. Many experimental studies report coarse estimates of temperature differences (for example, annual means), often omitting measurement duration, frequency and statistics. Furthermore, the few efforts to examine temperature changes carefully have found that warming chambers can sometimes result in the cooling of plots[20] or can have unintended effects on daily and seasonal temperature regimes[19]. Such variation might confound experimental study data because plants are differentially sensitive to temperatures during different parts of the day and integrate temperature differentially over months and seasons[23]. Moving towards more relevant measures of temperature sensitivity should also be a future goal for observational studies. For example, using MAT, we found that 23.4% of the species in the observational data responded significantly to temperature, but this proportion nearly tripled (to 67.6%) when a growing-degree day model was used (Supplementary Information). Additionally, researchers collecting experimental or observational data should report other environmental metrics that may drive phenology. For example, spring phenology is driven by snowmelt date in many alpine and tundra habitats[10, 24]. This date is not reported, however, at most sites, and experiments often remove warming structures in the snowpack season, thus not altering snowmelt date. Finally, we found high interspecific variation in sensitivities in both study types, suggesting that increased species sampling is needed for accurate climate change forecasting.

Our estimates of wild plant sensitivity to temperature, based on observations for 1,558 species, suggest that spring leafing and flowering will continue to advance at the rate of 5–6 days per °C in many regions of the world (within the limits of historical temperature ranges)[25]. The database underlying our estimates represents a sampling of species that is almost an order of magnitude higher than the most recent comprehensive meta-analysis of plant phenology[3]; yet sensitivity estimates using data derived from ref. 3 are highly similar to those presented here (Supplementary Information). Comparisons with temporal estimates (for example, the change in days per decade[5, 26]) are difficult; however, given a global increase in temperature of 0.6 °C over the past four decades[15], our estimates seem to be in line with the current estimates of −1.1 to −3.3 days per decade for plants[5].

Accurate models of biotic responses to climate change require comparable methods to estimate how plants shift with increasing temperatures. Field-based warming studies allow us to mechanistically test single versus multiple factors and to project forward to novel global conditions for which historical observations offer no comparisons[27]. To project experimental results, however, we must first verify that they match the changes that are observed in natural systems. Providing a first step, we have shown that warming experiments underpredict the advance of spring events observed over recent decades. Furthermore, when sampling the same species, the experiments failed to predict both the magnitude and the direction of plant responses to warming. Such differences between observed and experimentally estimated temperature sensitivities indicate that experimental results alone should not be used for parameterizing species distribution and ecosystem models. Although long-term observational data are currently the best measures of biotic responses to anthropogenic climate change[28], our results suggest that researchers may not understand these responses well enough to replicate them experimentally. Obvious remedies include ongoing efforts to improve experimental designs and to expand observational networks, improved prediction of species-level variation, and refinement and standardization of temperature sensitivities across experimental and observational studies.

Methods

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Complete methods are given in the Data and Methods sections of the Supplementary Information.

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Contributions

E.M.W. conceived the idea, performed analyses and wrote the paper. B.I.C. performed analyses. E.E.C. and N.J.B.K. assisted with analyses. E.M.W., E.E.C., J.M.A., T.M.C., S.E.T. and S.P. developed the STONE database. E.M.W., B.I.C. and J.R. contributed extensively to development of the NECTAR database. All authors (including J.L.B., T.J.D., T.R.A., K.B., S.J.M., G.J.M., B.J.M., C.P., N.S. and M.D.S.) contributed to the editing of the manuscript and to data management of the observational data sets.

Competing financial interests

The authors declare no competing financial interests.

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Supplementary information

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PDF files

1. Supplementary Information (712K)
This file contains Supplementary Text including Supplementary Data, Supplementary Methods and Supplementary Results. Also included are Supplementary Tables 1-6, Supplementary Figures 1-9 and additional references.

Zip files

1. Supplementary Data (3.1M)
This file contains the raw sensitivities that are shown in Figure S2c, which are from the PEP725 database and which are discussed in the Supplementary Data, Methods and Results.

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